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The Ciliary Ganglion of Birds.

By

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(With 2 fig. in the text and Plates XV and XVI.)

Anatomists are accustomed to assign the ganglia found outside the central nervous system of vertebrates either to the cerebro-spinal or to the sympathetic systems of peripheral nerves. Most ganglia fall readily into one or the other series, since the evidence furnished by their topographical relations, histological structure, and developmental history admits of no question as to their classification. There is, nevertheless, one peripheral accumulation of ganglion cells concerning which anatomists cannot yet be said to be in agreement. This is the ciliary ganglion of the head, first described by Schacher in 1701, and assigned by Arnold in 1831 to the sympathetic system, where, however, it has not been allowed to rest in peace. Schwalbe in 1879, after extensive anatomical studies embracing all classes of vertebrates, concluded that the ganglion belonged to the cerebro-spinal series, and that the oculomotorius, with which it is primarily connected, deserved to rank as a complete segmental nerve. Two years later W. Krause stated his opinion that, while in lower vertebrates the ciliary ganglion appeared to be the homologue of a spinal ganglion, in mammals it must be regarded as a composite structure, formed in part of cerebro-spinal, in part of sympathetic elements. Very recently v. Lenhossék (:10, :11) has reached the conclusion that the ganglion, from the standpoint of its histological structure, conforms neither to the cerebro-spinal nor sympathetic type, but must be regarded as a ganglion sui generis. Meanwhile, the original view of Arnold as to its purely sympathetic nature has not lacked supporters among recent investigators, and especially in the domain of human anatomy has this view held its ground (see, for instance, Müller und Dahl, :10).

The present investigation of the finer structure of the ciliary ganglion in birds has been carried on by means of different methods, the most successful of which have been the methylene blue intra-vitam staining and the silver impregnation of Cajal. Sections stained with Weigert's haematoxylin, acid fuchsin, and methylene blue (for Nissl-bodies) have also been studied, as well as teased preparations. Care has been taken to examine a number of serial sections, including not only the whole ganglion, but also surrounding structures lying in the orbit. In this way all connections of the ganglion with adjacent nerves have been determined.

The observations have been confined to three representatives of the group of birds: the hen, duck, and pigeon. The largest number of preparations, and the most successful ones, were made from material obtained from the hen, and the following account is based almost exclusively on that form. I have no reason to believe that the histological conditions in the ciliary ganglia of the duck and pigeon differ essentially from those described below.

While the present investigation was in progress, v. Lenhossék's interesting article on the same subject appeared in the Archiv für mikroscopische Anatomie for February, 1911. Frequent references to this paper will be found in the following pages, and as the account proceeds, it will become apparent to what extent my observations and interpretations agree or disagree with those of v. Lenhossék.

I wish to express my thanks to the directors of the Anatomo-Biological Institute in Berlin and the Zoological Institute in Munich for privileges enjoyed in their laboratories, and to Professor Rudolf Krause and Professor Ludwig Neumayer for friendly interest taken in the preparation of this paper.

Connection of the Ciliary ganglion with the Oculomotor Nerve. An ordinary dissection of the orbital nerves of the hen reveals in the vicinity of the ciliary ganglion the conditions shown in Figure 1. The abducent nerve passes through this region, but has been omitted in the drawings, since it is in no way connected with the ganglion in question. The oculomotor nerve (n. oc'mot.) gives off behind the eyeball a small branch (rm. mu. rt. d.) to the dorsal rectus muscle, and then turns ventral to run along the floor of the orbit to its termination in the ventral oblique muscle. As it bends downward the nerve sends a small ramus (rm. mu. rt. v.) to the ventral rectus muscle. Between these branches to dorsal and ventral eye muscles lies the spindle-shaped ciliary ganglion (gn. cil.) approximately 2 mm. in length, with its proximal (caudal) end in direct contact with the trunk of the third nerve. In my dissections a radix brevis has never been observed, and this lack of a special bundle of fibers between the nerve stem and the ganglion has been verified in eleven series of sections, which show (Fig. 2) that the most proximal ganglion cells are in contact with the oculomotor neurites extending into the ventral prolongation of the nerve. These neurites run nearly at right angles to the axis of the ganglion. My observations in regard to the absence of a radix brevis are in accord with those of Holtzmann ('96), but differ from those of v. Lenhossék (:11), who figures for the ciliary ganglion of the hen a distinct short root free from ganglion cells. In the light of my experience this appears to be an exceptional condition. Sections through the ciliary ganglia of the pigeon and duck show that in these forms also (as Holtzmann likewise observed) the ganglion is placed directly on the trunk of the third nerve.

Connection of the Ciliary Ganglion with the Ophthalmic Division of the Trigeminus. From the distal (cephalic) end of the ciliary ganglion a comparatively large nervus ciliaris brevis (Fig. 1, n. cil. brev.) proceeds directly to the eyeball. Microscopical examination shows that this large nerve (nervus ciliaris crassus of Holtzmann) is accompanied by a variable number of smaller fiber bundles. These arise from the main nerve as it emerges from the ciliary ganglion, or one or more of these smaller nerves may spring directly from the end of the ganglion itself.

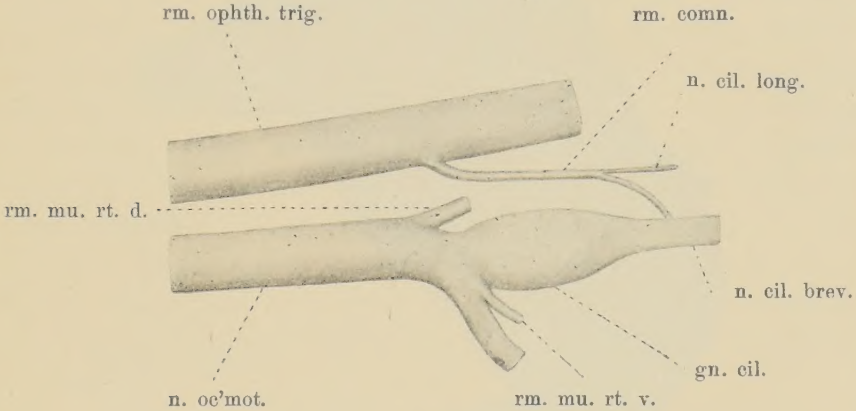

Fig. 1.

Dissection of the ciliary ganglion and connecting nerves in the hen. Gn. cil., ciliary ganglion; n. cil. brev., short ciliary nerve (nervus ciliaris crassus); n. cil. long., long ciliary nerve; n. oc'mot., oculomotor nerve; rm. comn., communicating ramus; rm. mu. rt. d., branch to dorsal rectus muscle; rm. mu. rt. v., branch to ventral rectus muscle; rm. ophth. trig., ophthalmic division of trigeminal nerve.

In dissections a slender communicating ramus (rm. comn.) from the ophthalmic division of the trigeminus may readily be observed passing to the nervus ciliaris crassus, with which it appears to unite about one mm. distal to the ciliary ganglion. This communicating ramus gives off one, sometimes two, nervi ciliares longi (n. cil. long.), which run to the eyeball with the nervi ciliares breves from the ciliary ganglion.

The further course of those fibers of the communicating ramus which reach the neighbourhood of the nervus ciliaris crassus can be followed only in sections. The microscope shows that about three-fourths of them pass forward to the eyeball; but it also reveals the interesting fact that the remaining fibers turn caudal, and, running parallel with the short ciliary nerves, enter the distal or cephalic end of the ciliary ganglion (rad. long., Fig. 2 and 15). The recurrent bundle constitutes, therefore,

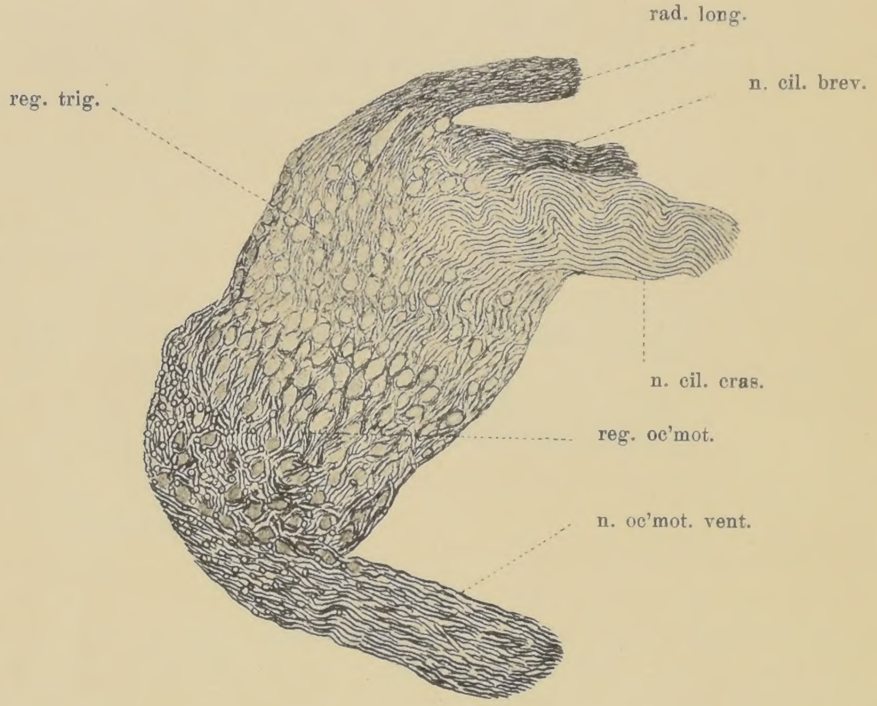

Fig. 2.

Longitudinal section through the ciliary ganglion of the hen. N. cil. brev., small short ciliary nerve composed of fine fibers from the trigeminal region; n. cil. cras., large short ciliary nerve (nervus ciliaris crassus) from the oculomotor region; n. oc'mot. vent., ventral continuation of oculomotor nerve; rad. long., long root of ciliary ganglion from communicating ramus of ophthalmic division of trigeminus; reg oc'mot., oculomotor region of ganglion; reg. trig., trigeminal region of ganglion.

a radix longa ganglii ciliaris. It is made up of very fine, slightly medullated fibers, and is often closely associated with one of the smaller ciliary nerves, the two bundles sometimes being bound together in the same perineural sheath. The other fibers of the communicating ramus — those which pass as long ciliary nerves to the eyeball — are also of very small caliber, and but weakly medullated. When the ramus is followed back to its origin from the ophthalmic division of the trigeminus, it may be observed to run central for a short distance as a distinct bundle lying just under the perineurium of the ophthalmic nerve. Still farther central the bundle loses its identity, as its fibers gradually become mixed with those of the nerve trunk. Many of the latter fibers are as small in diameter as those of the ramus.

A radix longa, i. e., a communicating nerve between the trigeminus and the ciliary ganglion, was first described as present in the hen by Holtzmann ('96), who, however, influenced possibly by Schwalbe's views as to the relation of the ganglion to the oculomotorius, did not consider it of physiological importance. He looked upon it as a remnant of an embryological condition. That a communicating ramus passing directly to the ganglion occurs in chick embryos was pointed out by D'Erchia ('95), and verified later by the present writer. v. Lenhossék, however, in his recent investigation, failed to find fibers representing a radix longa in the hen, and is of the opinion that the oculomotor nerve furnishes the only central connection of the ganglion.

Zeglinski ('85) and Jegorow ('86—87) have described for adult pigeons a direct nervous connection between the fifth nerve and the ciliary ganglion. Their observations on these birds I can corroborate. In my sections the communicating ramus runs to the cephalic end of the ganglion, and here divides. Part of its fibers enter the ganglion, and part turn forward to accompany the nervus ciliaris crassus to the eyeball.

In agreement with v. Lenhossék and other investigators I have been unable to discover in the birds examined the slightest trace of a sympathetic root of the ciliary ganglion. The possibility exists, it is true, that the fibers which enter the ganglion from the communicating ramus are really sympathetic fibers which have joined the trigeminus somewhere along its course; but at least no independent nerve belonging to the cephalic extension of the sympathetic system enters the ciliary ganglion, as is the case in man and other mammals. The probable nature of the fibers of the radix longa will be discussed later.

The Oculomotor and Trigeminal Regions of the Ciliary Ganglion. When a longitudinal section of the hen's ciliary ganglion is examined under a lens of moderate power, two regions may be distinguished. Figure 2 is a drawing of such a section, stained by the Cajal silver method, and cut in an especially favorable plane. It will be seen that the proximal end of the ganglion is invaded by the coarse, heavily medullated, darkly stained neurites of the oculomotor nerve. These fibers, winding in among the cells, may be followed distally into the central part of the ganglion, where they gradually give way to the finer, less heavily medullated, and less deeply stained neurites of the nervus ciliaris crassus (main short ciliary nerve). To this portion of the ganglion, related thus to the oculomotor nerve, we may for convenience apply the name of oculomotor region (reg. oc'-mot.). It comprises approximately three-fourths of the whole structure.

Turning our attention now to the radix longa (rad. long.) we find that the fibers from the communicating ramus of the trigeminus enter the remaining fourth of the ganglion at its distal end. These very fine and only slightly medullated fibers give the portion of the ganglion they supply (reg. trig.) a lighter and more finely fibrillar appearance than that presented by the oculomotor region. Darkly stained, heavily medullated fibers, such as those of the oculomotor nerve, are completely absent. This area will hereafter be referred to as the trigeminal region. From it emerges a bundle of neurites (n. cil. brev.), which accompanies the nervus ciliaris crassus cephalad, at first closely applied to it, but farther on separating from it to form a small independent ciliary nerve. The fibers of this bundle are smaller and less well medullated than those of the large ciliary nerve they accompany.

The limits of the two regions just described are not, it is true, sharply defined. One area merges gradually into the other with some intermixture of the elements characteristic of each. In their central portions, however, they are distinctly unlike. As will shortly be seen they can be further differentiated by the peculiar types of nerve endings found in connection with their ganglion cells.

The Ciliary Ganglion Cells. The cells of the hen's ciliary ganglion are apparently all unipolar, as first definitely determined by v. Lenhossék (:10, :11). With that author's full description of their characters my observations agree. The single process springs from one pole of the somewhat elliptical cell (Fig. 5 and 10), and soon acquiring more or less medullation, passes without branching into a ciliary nerve. A T-shaped division of the process, such as is characteristic of the neurones of spinal ganglia, has never been observed. The ganglion cells are inclosed in capsules rather abundantly supplied with amphicyte or satellite nuclei. A conspicuous accumulation of amphicyte nuclei is frequently found near that pole of the cell from which the neurite takes its origin. Dendrites appear to be completely absent.

Nerve Endings in the Oculomotor Region. The neurites of the oculomotor nerve show, in their terminations about the cells of the ciliary ganglion, at least three different types of end structures. These are connected, however, by intermediate forms. In the classification of the types of endings I follow v. Lenhossék in the main, but without including, as he does, the fine, net-like terminations of the fibers of the radix longa in the category of oculomotor endings.

The most striking and peculiar as well as most abundant type is the calyx ending (Fig. 3, 4, 5, 6). The comparatively coarse oculomotor neurite expands on reaching the ciliary ganglion cell into a cup-shaped termination or calyx, with a variable number of sepal-like processes. The calyx embraces that pole of the cell from which the neurite arises. The ending is intracapsular, as shown by Figure 6, and is so closely applied to the cell as to suggest the fingers of the hand grasping a round object of convenient size. The finger-like or sepal-like processes differ in length. They are usually confined to one half of the cell, but one or more may extend as far as the opposite pole. Usually they end freely, but they may approach and unite to form one or more loops. Occasionally they break up into a small number of terminal knobs. The circle of processes extends all the way around the ganglion cell, as may readily be determined in methylene blue sections by focussing through the faintly stained and fairly transparent cell-body. In the drawings only the upper surfaces of the cell-bodies have been represented. The methylene blue staining, while not as satisfactory for the nerve cells (at least in my preparations), brings out the details of these calyx endings better than the silver method employed by v. Lenhossék. This author describes the terminations as „gabelförmige Endigungen", each being composed of a triangular basal expansion from which two, or more rarely three, unbranched processes run meridionally over the surface of the cell, but without reaching the opposite pole. Methylene blue staining demonstrates the calyx-like form of the ending, and shows that the processes are often as many as six, and even more, in number. v. Lenhossék recognized the resemblance to the „Endkelche" of Held in the nucleus trapezoides of mammals. Since he found the „gabelförmig" ending more abundant in a 21-day chick than in adult fowls, he looks upon it as a „primitive Form", from which the other types of terminations take their origin.

A second type of oculomotor termination is the brush ending (Fig. 7 and 8), to which we pass from the calyx form through intermediate gradations. The heavy oculomotor neurite breaks up, before reaching the ganglion cell, into two or three main branches, which may again subdivide. These forkings are applied to the surface of the cell-body, chiefly on the side approached by the neurite, though not infrequently the terminal fibrils extend to the opposite side. The tips of the ultimate branches are sometimes expanded into small terminal knobs. This „büschelformig" type of ending, as v. Lenhossék has pointed out, is usually associated with a flattening or indentation of the pole of the cell with which it is in contact.

A third variety of ending found in this region is called by v. Lenhossék a „polares Geflecht", but I prefer to designate it as an arborescent ending, since I cannot convince myself that anastomoses occur between its numerous branches. This type, illustrated by Figure 9, is plainly a development of the brush ending just described. The subdivision of the main end branches of the oculomotor fiber is carried to a greater extent, the result being a complicated arborization, the fine branchlets of which cross one another in various directions, but probably do not unite to form a veritable network. The question of the existence of true end plexuses about the cells of the oculomotor portion of the ganglion will be discussed after the description of the type of ending which characterizes the trigeminal region.

Nerve Endings in the Trigeminal Region. The fibers which enter the ciliary ganglion from the ramus communicans trigemini terminate on the nerve cells situated in the portion of the ganglion described above as the trigeminal region. The cells here are also unipolar (Fig. 10). The amphicyte nuclei found in their capsules are usually evenly distributed. The endings of the fibers of the radix longa never take the forms just described for the oculomotor region. They are always end nets or plexuses (Fig. 11, 12, 13). The fine trigeminal fiber, easily told from the large oculomotor neurite by its smaller size (compare Fig. 3 to 9 with Fig. 12 and 13), gives rise by branching to an intracapsular, pericellular complex of fibrils. These are arranged in an irregular way over the surface of the cell, and apparently anastomose to form true networks or plexuses. Here and there along the fibrils may be seen small expansions which appear granular under the oil immersion. In many cases short side branches are given off, which end freely in slight terminal swellings, also distinctly granular in appearance. These terminations are not always in contact with the surface of the cell, but may lie in the space between the latter and its capsule, where amphicyte nuclei are also found. v. Lenhossék (:11), in describing such a relation between the arborescent endings of the oculomotor fibers and the nerve cells, suggests that this arrangement may indicate that the nervous impulse passes from one neurone to the other by means of a kind of induction.

The trigeminal region of the hen's ciliary ganglion is, then, characterized by these end nets. In the cephalic and central portions of the region only end nets are present — not a single end calyx or other oculomotor termination is to be seen. But as we approach, in the caudal or proximal direction, the zone lying between the trigeminal and oculomotor areas, we meet with an intermixture of the elements typical of the two regions. The coarse, heavily medullated fibers of the third nerve mingle with the slender fibers from the trigeminus, and calyx endings lie side by side with end nets. Still farther caudal the predominance of heavy oculomotor neurites and their characteristic endings becomes marked.

I am not, however, prepared to say positively that the oculomotor fibers never end in true nets or baskets around the ciliary ganglion cells. Here and there in the oculomotor region one can make out an occasional end net, especially near the surface of the ganglion. But I have never been able to see, in my sections, a connection between one of these and an oculomotor neurite. Whenever the conditions have permitted me to observe the fibers giving origin to the end nets, these have proved to be of the fine, scantily medullated, trigeminal variety, and not in the least like the heavy, conspicuous, oculomotor fibers, so easily traceable into calyx endings. The truth of the matter may be that a few of the slender fibers of the long root stray from the trigeminal region proper into adjacent, and, peripherally, even into distant portions of the ganglion, to end there in typical pericellular plexuses.

v. Lenhossék (:11), while admitting that at first glance these endings appear to be essentially different from those previously described, declines to consider them as belonging to a special category. Since he does not recognize a radix longa from the trigeminus, he looks upon them as oculomotor endings, although his figures show a striking difference in size between the fibers giving size to the nets and those heavy neurites of the third nerve which terminate in other ways. In support of his view he states that intermediate stages exist between this form and the arborescent type (v. Lenhossék's „polares Geflecht"). This observation I cannot verify in my preparations. The pericellular plexuses are, according to his account, already present in a 21-day chick around cells arranged in groups, especially in the peripheral parts of the ganglion. They therefore appear to be quite as primitive forms as the calyx („gabelförmig") endings, which are also present at this time, and which he regards as developmental stages in the growth of the more complicated types.

Ganglion Cells from Teased Preparations. The first descriptions of the cilary ganglion cells of the hen were based on teased preparations made after the ganglionic tissues had been allowed to undergo slight maceration. Retzius ('80) described these cells as bipolar, both processes being medullated and arising near together. Holtzmann ('96) confirmed the observations of Retzius, although be obtained many unipolar cells in Golgi preparations made from young chicks. The writer (Carpenter, :06) also described the ciliary cells as bipolar after studying teased fragments of the ganglion. Occasional unipolar cells were regarded as multilated elements from which one of the processes had been torn away by the needles.

The application of more modern staining methods now makes it clear that these interpretations were erroneous. These cells are from the oculomotor region of the ganglion, and one of the supposed processes is a foreign fiber ending on the cell-body in the form of a firmly affixed calyx, which often successfully resists the teasing needle. As is shown in Figure 14, a somewhat macerated cell stained in acid fuchsin and isolated by teasing gives little evidence of the exact relation between it and the two fibers with which it is connected. The study of methylene blue and silver preparations has taught us, however, to recognize in the fiber showing the heaviest axis cylinder an oculomotor neurite, while the more slender medullated axone is unquestionably the process arising from the cell, i. e., a ciliary neurite.

Physiological Significance of Calyx Endings. By means of their expanded calyx endings the oculomotor neurites are brought into close contact with comparatively large surface areas of the ganglion cells. The break in the continuity of the two neurones is much less than that found in a typical sympathetic ganglion, where pericellular plexuses of fine fibrils convey the nervous impulse from the preganglionic fiber to the postganglionic or sympathetic neurone. Reasoning from the anatomical conditions one might predict greater difficulty in interrupting the nervous impulse in the ciliary ganglia of birds than in ganglia typically sympathetic in their synaptic relations. That this has been the experience of experimenters, the following citations will show.

It is well known, from the researches of Langley, that a small quantity of nicotin will prevent the passage of nervous impulses through sympathetic ganglia, while spinal ganglia, in which the path is not broken by synapses, remain unaffected This inhibition in sympathetic ganglia is believed to be due to the paralyzing effect of the drug on the pericellular baskets around the sympathetic cells. The ciliary ganglion of mammals, in which the oculomotor fibers end in pericellular networks (Michel, '94; Sala, :10; v. Lenhossék, :10) responds readily to nicotin, behaving in this respect like a sympathetic ganglion (Langley and Anderson, '92, Marina, '99). The ciliary ganglion of birds, on the contrary, resists the action of nicotin nearly as successfully as a spinal ganglion. Consiglio (:00), as reported by Langendorff (:00), subjected the ciliary ganglion of birds to nicotin, but found that stimulation of the third nerve was still followed by constriction of the pupil, i. e., the nervous impulses were not interrupted in the ganglion. Langendorff, himself, observed that after death by bleeding the ciliary ganglion of mammals lost its capacity to transmit impulses before the short ciliary nerves became inactive. This he believed to be due to the intercalation of ganglion cells between the fibers of the oculomotorius and the nervi ciliares breves. The condition is typically sympathetic. When he experimented upon a duck he obtained quite different results. The ciliary ganglion, deprived of blood, continued for about 12 minutes to permit the passage of impulses originating in the third nerve. When stimulation of the latter no longer affected the iris, stimulation of the nervus ciliaris crassus, i. e., a postganglionic nerve, was equally ineffective. Langendorff's conclusion was that the fibers of the oculomotorius in birds do not terminate in the ciliary ganglion, since the physiological evidence points to the continuity of the transmitting apparatus. This he believed to be effected by means of bipolar ganglion cells, each of which sends one process caudal into the oculomotor nerve, and the other cephalad into the short ciliaries. In this view he was supported, as has been mentioned, by the anatomical findings of Retzius and Holtzmann.

In the light of our present knowledge of the histological structure of the bird's ciliary ganglion its exceptional behavior is readily explained in a quite different manner. The oculomotor neurites unquestionably terminate in the ganglion, but their grasp, so to speak, on the next set of neurones is, by means of calyx endings, so intimate and comprehensive that a practically uninterrupted path is offered for the nervous impulse. The ganglion, therefore, resists nicotin and bleeding, while sympathetic and mammalian ciliary ganglia, with less binding synapses between their neurones, yield readily to these influences.

Functions of the Fiber Bundles entering the Ciliary Ganglion. In Figure 15 I have represented in a diagrammatic way the histological relations between the ganglion and the fiber bundles connected with it. It can there be seen at a glance that we have to do with two systems of neurones, an oculomotor and a trigeminal, each of which contains pre- and postganglionic elements, the cell-bodies of the latter being situated in the ganglion. If it be admitted that the foregoing account warrants this conception of the anatomical relations, we may pass to the consideration of the physiological significance of the tracts represented.

As to the function of the oculomotor system there can be no question. Investigators are agreed that stimulation of the third nerve causes contraction of the pupil. Therefore the fibers entering the ganglion from the oculomotorius, and the postganglionic ciliary neurones connected with them, are efferent or motor, and subserve the function of pupil constriction.

It is much more difficult to decide in respect to the nature of the trigeminal component. We have as a premise for our reasoning the observations of Zeglinski ('85) to the effect that direct stimulation of the trigeminal nerve consistently causes dilatation of the pupil. This reaction is obtained in mammals by excitation of the cervical sympathetic. In birds, however, such stimulation produces either no effect on the iris (Zeglinski, '85, Jegorow, '87) or at most one which is slight and inconstant (Langley, :03ª). Zeglinski is convinced that in birds all the pupil-dilator fibers, whatever their origin may be, reach the eye through the ramus ophthalmicus trigemini.

What, then, is the probable source of these fibers? Are they sympathetic or do they belong to the motor root of the trigeminus? Microscopical examination fails to furnish the answer, since in the hen sympathetic fibers cannot be distinguished from fine cerebro-spinal fibers, the former as well as the latter being provided with medullary sheaths. If the pupil-dilator fibers of the ophthalmicus are sympathetic in origin it is difficult to understand why stimulation of the cervical sympathetic trunk, with which they should be connected, fails to produce an effect on the iris. On the developmental side it has been shown (Carpenter, :06) that in chick embryos the fibers of the ramus communicans grow toward and connect directly with the anlage of the ciliary ganglion during the fifth day of incubation. At this time, at least, the ophthalmic division of the trigeminus shows no sympathetic connections.

The evidence at our command seems to be in favor of our regarding the pupil-dilator fibers running in the ophthalmicus as cerebrospinal neurones belonging to the motor component of the trigeminal nerve. Can we follow the impulse which passes along them to the dilator muscle of the iris? Does it travel by the long ciliary nerves given off by the ramus communicans, or does it pass into the ciliary ganglion via the radix longa, and thence along short ciliary fibers to the eyeball? Here we are driven to reasoning by analogy, since we possess no data bearing directly on this point. We have seen that the pupil-constrictor system is made up of two sets of neurones, preganglionic (oculomotor) and postganglionic (short ciliary). There may be some requirement of this pupillary reflex mechanism which demands, along the motor limb of the arc, a second, peripheral neurone connected with the end organ. These conditions are met by the radix longa and the short ciliary fibers continuous with it, while they are not met by the long ciliary nerves. We are perhaps warranted, therefore, in looking upon the path through the ciliary ganglion via the radix longa as the one taken by the efferent impulses in the reflex causing dilatation of the pupil. This assumption that the fibers of the long root are motor leaves the long ciliary fibers of the communicating ramus as the sensory component of the trigeminal innervation of the eyeball.

Nature of the Ciliary Ganglion of Birds. With the foregoing analysis of its structure and connections before us, in what light are we to regard the ciliary ganglion of birds? Is it a cerebro-spinal ganglion, a sympathetic ganglion, a combination of the two, or a ganglion sui generis?

The ganglion in birds is plainly not cerebro-spinal, because: (1) it does not originate from the neural crest (Carpenter, :06); (2) the processes of its cells do not show T-shaped divisions, with one branch entering the central nervous system; (3) it lies on the trunk of a motor nerve, some of the neurites of which end on its cells; (4) it appears to be purely motor in function.

The ganglion is not sympathetic in the sense that it is the most cephalic representative of the ganglia of the sympathetic chain, because: (1) there is no evidence that its cells are in any way connected with the cervical sympathetic; (2) the cells are unipolar, not multipolar, as are the sympathetic cells, and they are in large part embraced by calyx endings or modifications of these, which are unknown in the sympathetic system; (3) the ciliary ganglion cells are on the average somewhat larger than sympathetic cells, and have better developed capsules with amphicyte nuclei; (4) it is probable that the ganglion receives no sensory fibers comparable with those contributed by the spinal ganglia to the sympathetic system.

It follows as a corollary from these considerations that the ciliary ganglion of birds cannot be looked upon as a composite cerebro-spinal and sympathetic ganglion.

Are we then to accept v. Lenhossék's conclusion that it is a ganglion sui generis? Although v. Lenhossék overlooked the connection with the trigeminus, and consequently could not form a complete conception of the relations of the ganglion, he nevertheless acquired sufficient evidence from its histological structure to show that it is neither cerebro-spinal nor sympathetic. His conclusion was based partly on the erroneous view that he was dealing with „ein Ganglion, das mit dem Sympathicus und Trigeminus nichts zu tun hat, sondern ganz und gar dem Oculomotorius angehört"; but as we have seen the connection with the fifth nerve, which undoubtedly exists, does not essentially alter the case. The structure still remains in all probability „ein rein motorisches Ganglion".

While agreeing with the general conclusion of v. Lenhossék, and holding that the ciliary ganglion of birds does not belong to the sympathetic system proper, I see no reason why it should not be included in the autonomic nervous system as proposed by Langley. As a ganglion receiving preganglionic and giving off postganglionic fibers, i. e., interposing a second set of neurones in the course of a motor path from the central nervous system, it conforms to the general description given by Langley (:03^b) for the autonomic ganglia. This author separates the autonomic system into four subdivisions, viz., the mid-brain autonomic, the bulbar autonomic, the sympathetic, and the sacral autonomic. He shows that the various members of the system have certain characteristics in common, but points out that, phylogenetically, they may have arisen independently. He thus prepares us for such variations in structural details as we find in the ciliary ganglion of birds when we compare it with a sympathetic ganglion of the truuk region.

Ontogenetically the ciliary and sympathetic ganglia in the group of birds seem closely related. In a former paper, previously quoted, the writer has described the development of the ciliary ganglion in the chick from cells which migrate from the mid-brain along the oculomotor nerve, and from the Gasserian ganglion along the ophthalmicus and ramus communicans. Recently Kuntz (:10) has found evidence in chick embryos that the sympathetic ganglia develop in a similar way, receiving part of their cells from the neural tube by migration along the ventral roots of spinal nerves, and part from spinal ganglia via the dorsal roots.

It is not improbable that all parts of the autonomic system have arisen in phylogenesis in somewhat the same manner, through a peripheral migration of cells from more central structures. Varying demands in different regions of the body have called forth the appropriate autonomic nervous mechanisms, and it is not surprising that the unlike conditions under which these have arisen find their expression in dissimilarities in structural details.

In spite, then, of certain differences in internal structure and topographical relations, the ciliary ganglion of birds falls into the same general system with the sympathetic ganglia. It is the most anterior of the autonomic series, and, by virtue of its oculomotor and trigeminal connections, belongs to the mid-brain and bulbar subdivisions of this system.

Summary. This summary is based largely on results obtained from the study of the ciliary ganglion in the hen.

1. The ciliary ganglion of birds is closely related to the oculomotor nerve. In the hen, pigeon, and duck the ganglion is situated directly on the trunk of the nerve, i. e., no short root normally exists.

2. The ganglion gives off from its distal end one large nerve and a variable number of smaller ones. These together constitute the nervi ciliares breves.

3. A communicating ramus from the ophthalmic division of the trigeminus joins the nervi ciliares breves not far from the ganglion. About three-fourths of the fibers of this ramus accompany the short ciliary nerves to the eyeball (nervi ciliares longi). The remaining fibers turn caudal and enter the distal end of the ganglion, thus forming a radix longa.

4. A sympathetic root is not present.

5. The cells of the ciliary ganglion are unipolar. Their unbranched processes (neurites) pass distally to form the short ciliary nerves. The cell bodies are inclosed in capsules with amphicyte or satellite nuclei.

6. Large, well medullated fibers from the oculomotorius enter the proximal portion of the ganglion, and terminate on about three-fourths of the cells in calyx, brush, or arborescent endings. Whether these fibers ever terminate in true end nets is doubtful. The portion of the ganglion supplied by the oculomotor nerve is characterized by the presence of coarse, heavily medullated neurites and the peculiar endings just mentioned. It may be designated the oculomotor region. The short ciliary neurites emerging from this region are of small caliber, but have comparatively large medullary sheaths.

7. Fine, weakly medullated fibers forming the radix longa from the ophthalmicus enter the distal portion of the ganglion, and terminate on cells here in the form of delicate end nets. This may be called the trigeminal region. Heavily medullated fibers and the endings peculiar to the oculomotor region are absent. The short ciliary neurites emerging distally are less well medullated than those from the oculomotor region, and often form a special bundle running as a small nervus ciliaris brevis to the eyeball.

8. The failure of nicotin and removal of blood to paralyze the ciliary ganglion of birds is probably due to the calyx endings which intimately bind together the oculomotor and ciliary neurones.

9. The trigeminal fiber system (radix longa and short ciliary neurones) passing through the ganglion appears to be motor in function, and to control the dilator muscle of the iris. The morphological and experimental evidence at command points to the cerebro-spinal (trigeminal) nature of the fibers of the radix longa, rather than to their sympathetic nature.

10. The ciliary ganglion of birds is not cerebro-spinal, nor, strictly speaking, sympathetic. It appears to be a purely motor ganglion, with peculiar histological characters, belonging to the mid-brain and bulbar subdivisions of the autonomic nervous system.

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Explanation of Plates.

Figures 3 to 14 are drawings of cells and nerve terminations in the ciliary ganglion of the hen as seen under a 2—mm. oil immersion objective. As far as practicable the illustrations have been made with the aid of a camera lucida. Figures 3 to 9 show endings of oculomotor fibers; Figures 11 to 13, endings of trigeminal fibers.

Plate 1.

Fig. 3 and 4.	Calyx endings. Methylene blue.
Fig. 5.	Calyx ending. Cajal silver method.
Fig. 6.	Calyx ending. Methylene blue and alum carmine. The cell-body and cell capsule with amphicyte nuclei are stained red.
Fig. 7.	Brush ending. Methylene blue.
Fig. 8.	Brush ending. Cajal silver method.
Fig. 9.	Arborescent ending. Cajal silver method.
Fig. 10.	Ganglion cell from trigeminal region. Methylene blue.

Plate 2.

Fig. 11.	End net. Methylene blue. Certain of the circular or oval granular bodies appear to be amphicyte nuclei which have taken the blue stain. Others are plainly expansions of the nerve fibrils.
Fig. 12 and 13.	End nets. Methylene blue and alum carmine. The cell bodies and amphicyte nuclei are stained red.
Fig. 14.	Isolated cell from a macerated and teased preparation of the ciliary ganglion. Acid fuchsin. The coarse medullated fiber is an oculomotor neurite, ending probably in a calyx; the finer medullated fiber is a ciliary neurite arising from the cell-body.
Fig. 15.	Diagram of the ciliary ganglion and its connections in the hen, showing the relations of the oculomotor and trigeminal fibers to the ciliary neurones. N. cil. brev., short ciliary nerves; n. cil. long., long ciliary nerves; n. oc'mot., oculomotor nerve; neur. cil.[I], short ciliary neurone (pupil-dilator?); neur. cil.[II], short ciliary neurone (pupil-constrictor); neur oc'mot., oculomotor neurone (pupil-constrictor); neur. trig.[I], trigiminal neurone (pupil-dilator?); neur. trig.[II], trigeminal neurone (sensory?); rad. long., long root; reg. oc'mot., oculomotor region of ganglion; reg. trig., trigeminal region of ganglion; rm. comn., ramus communicans; rm. ophth. trig., ophthalmic division of trigeminal nerve.

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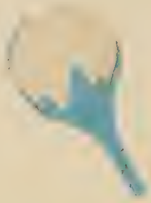

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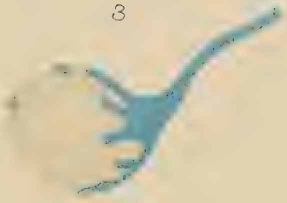

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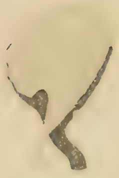

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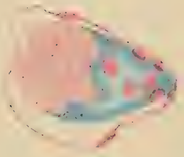

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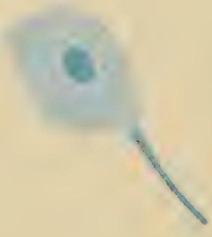

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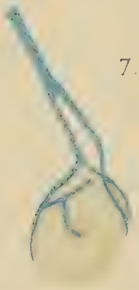

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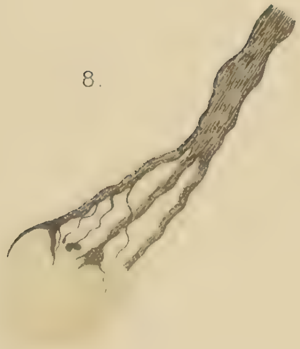

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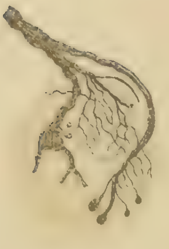

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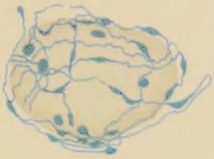

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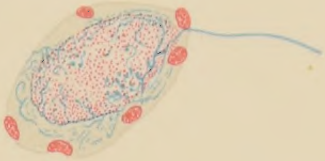

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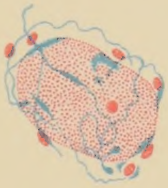

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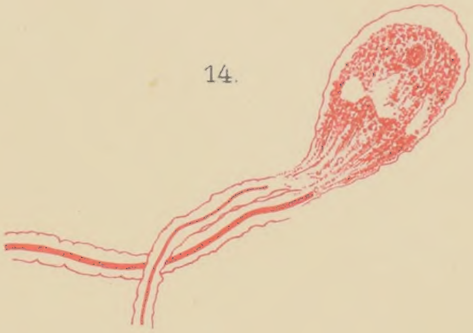

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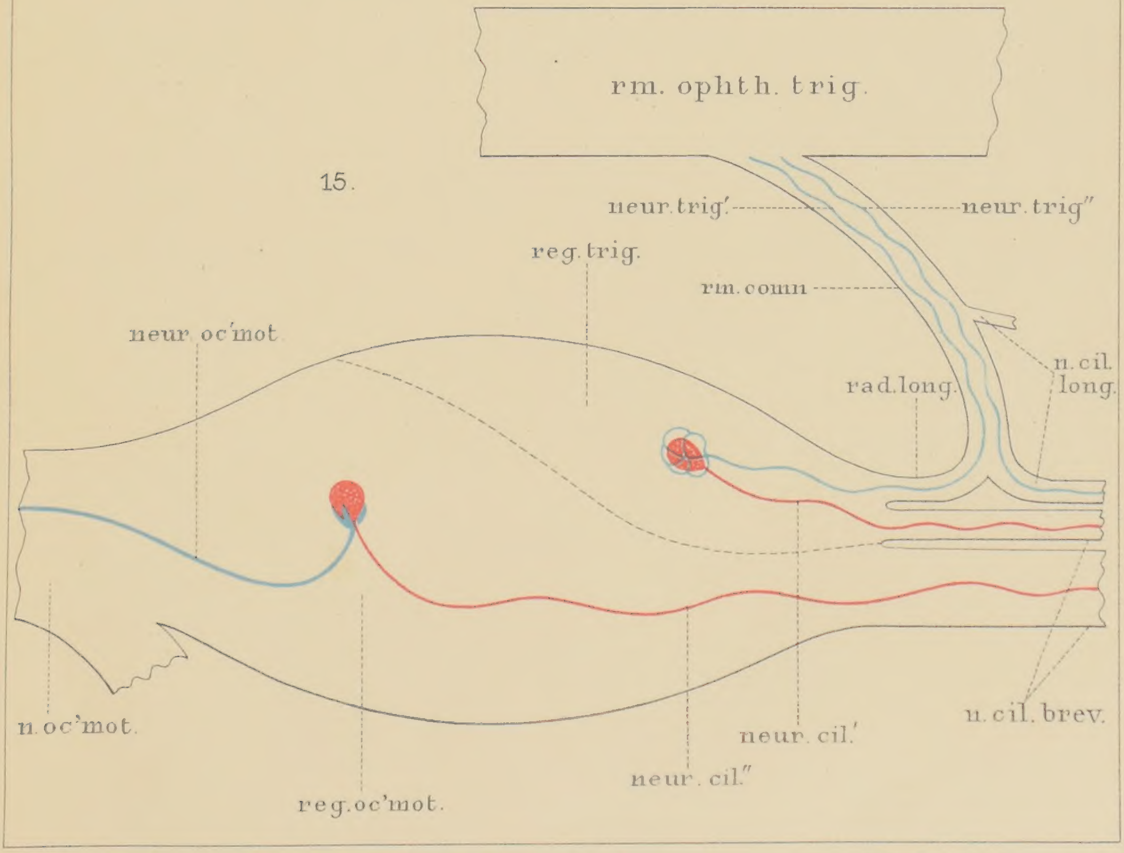

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